

Critical comments on the phylogenetic relationships within the family Papilionidae (Lepidoptera)

Christoph L. HÄUSER

Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 150-164, D-53113 Bonn 1, Germany.

Summary

The current hypothesis about the phylogenetic relationships within the family Papilionidae is critically re-examined on the basis of available information about the exact distribution of individual characters. The position of the genus *Hypermnestra* within the subfamily Parnassiinae cannot be supported by any synapomorphy. The Parnassiinae are not recognizable as a monophyletic group even without the genus *Hypermnestra*, as all apomorphic character states also occur in the tribe Troidini of the Papilioninae. The monophyly of the Papilioninae still appears well supported, but two supposedly autapomorphic characters for this subfamily show incongruent distributions. The cubital crossvein in the forewing does not present an autapomorphy of the Papilioninae. An alternative and better supported cladogram for the Papilionidae cannot be presented until additional characters have been more carefully examined.

Zusammenfassung

Die aktuell als gültig angesehene Hypothese der phylogenetischen Verwandtschaftsverhältnisse innerhalb der Papilionidae wird anhand der genauen Verteilung bekannter Merkmale kritisch überprüft. Für eine Zugehörigkeit der Gattung *Hypermnestra* zur Unterfamilie Parnassiinae finden sich keine synapomorphen Merkmale. Die Parnassiinae lassen sich auch ohne die Gattung *Hypermnestra* nicht als Monophylum begründen, da alle als apomorph angesehenen Merkmalszustände auch innerhalb des Tribus Troidini der Papilioninae auftreten. Die Monophylie der Papilioninae scheint gegenwärtig besser begründbar, jedoch ist das Auftreten von zwei bisher als Autapomorphien angesehenen Merkmalen widersprüchlich. Die Cubitoanalkuerader im Vorderflügel stellt keine Autapomorphie der Papilioninae dar. Ein alternatives, besser begründetes Kladogramm der Phylognese der Papilionidae kann erst nach sorgfältiger Untersuchung weiterer Merkmale erarbeitet werden.

Résumé

L'hypothèse considérée actuellement comme valable en ce qui concerne les relations de parenté phylogénétique à l'intérieur de la famille des Papilionidae

fait l'objet d'un nouvel examen critique, basé sur la distribution exacte de caractères individuels connus. L'appartenance du genre *Hypermnestra* à la sous-famille des Parnassiinae ne peut être défendue par aucune synapomorphie. Même sans le genre *Hypermnestra*, les Parnassiinae ne peuvent être considérés comme un groupe monophylétique, étant donné que tous les états de caractères considérés comme apomorphique se rencontrent également dans la tribu Troidini des Papilioninae. La monophylie des Papilioninae semble actuellement mieux défendable, mais deux caractères considérés jusqu'à présent comme autapomorphies pour cette sous-famille présentent des distributions contradictoires. La nervure transversale cubito-anale de l'aile antérieure ne représente pas une autapomorphie des Papilioninae. On ne pourra présenter un cladogramme alternatif mieux fondé de la phylogénie des Papilionidae qu'après un examen approfondi de caractères supplémentaires.

Introduction

The Papilionidae or Swallowtail Butterflies can be said to represent one of the best known families of all Lepidoptera, and many species have been studied in great detail from an ecological, morphological, and systematic point of view (see Igarashi, 1979 ; Collins & Morris, 1985 ; Goyle, 1990). The phylogeny of the family Papilionidae is generally held to be well known, and the Swallowtails have been used as a key group to illustrate the concept of coevolution between specialized herbivores and their hostplants (Ehrlich & Raven, 1964 ; Miller, 1987a).

All recent systematic studies on the Papilionidae agree in principle about their higher classification and about the phylogenetic relationships within the family (Munroe, 1961 ; Hancock, 1983 ; Igarashi, 1984 ; Scott, 1985, Miller, 1987b). The purpose of this paper is to point out that the distribution of many of the characters previously used is incongruent with the currently accepted view of the phylogenetic relationships within the Papilionidae.

The Papilionidae and their systematics

The family Papilionidae comprises worldwide about 570 species, and is currently divided into three subfamilies, Baroniinae, Parnassiinae, and Papilioninae. The Baroniinae are monotypic, the Parnassiinae consist of two tribes, Parnassiini and Zerynthiini, with together about 60 species, and the remaining Papilioninae are usually divided into three tribes : the Troidini with about 140 species, the Graphiini (or Leptocircini) with about 150 species, and the Papilionini with about 220 species (Hancock, 1983 ; Collins & Morris, 1985 ; Miller, 1987b). In phylogenetic terms, all these taxa are assumed to be monophyletic,

and the Baroniinae are regarded as the sister group of the Parnassiinae and Papilioninae. Within the Papilioninae, the Graphiini are held to represent the sistergroup of the Troidini and Papilionini (see Fig. 1). Differences in opinion exist with regard to the position of the genera *Meandrusa* Moore, 1888 and *Teinopalpus* Hope, 1843, which are either placed in the Graphiini or in the Papilionini sensu lato (see Hancock, 1983 ; Miller, 1987b).

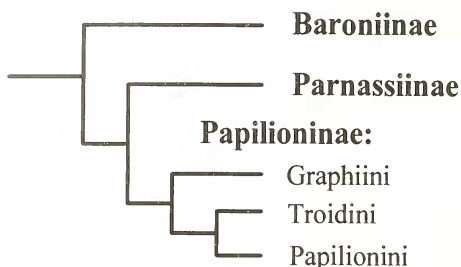


Fig. 1. Cladogram of the currently accepted hypothesis of the phylogenetic relationships within the family Papilionidae.

The monophyly of the Parnassiinae

During a critical re-examination of the characters used to support the currently accepted hypothesis of the phylogenetic relationships, problems were encountered to find autapomorphous characters which would allow to recognize the Parnassiinae as a monophyletic group (Häuser, 1990a). According to the present classification, the subfamily Parnassiinae comprises the following eight genera (species numbers in parentheses) : *Parnassius* Latreille, 1804 (35-42), *Zerynthia* Ochsenheimer, 1816 (2), *Archon* Hübner, 1822 (2), *Hypermnestra* Ménétriés, 1848 (1), *Sericinus* Westwood, 1851 (1), *Bhutanitis* Atkinson, 1873 (4), *Luehdorfia* Crüger, 1878 (3-4), and *Allancastris* Bryk, 1932 (3-4) (see Bryk, 1934-1935, Ackery, 1975 ; Hancock, 1983). The characters that have been previously used to define the Parnassiinae as a taxon, however, are all inconsistent with the present delimitation of this group.

First, most apomorphic character(-state)s of the Parnassiinae are not present in the genus *Hypermnestra* despite statements to the contrary (Scott, 1985 ; Hancock, 1983) ; these include asymmetrical pretarsal claws, a heavily sclerotized abdominal segment VIII in females, a long

and thin, strongly sclerotized aedeagus, and the occurrence of a sphragis (see below). *Hypermnestra* shows instead a number of highly unusual, presumably autapomorphic traits, such as two parallel downwards curved horns on the head of the fully grown larva, and a pair of longitudinally oriented, large serrated ridges on the mesothorax of the adult (Le Cerf, 1913 : 5-22). However, these traits do not support any close phylogenetic relationship with other genera of the Parnassiinae. From a phylogenetic point of view, therefore, the genus *Hypermnestra* cannot form part of a monophyletic group Parnassiinae and should probably be classified in a taxon of its own. This conclusion was reached independently by Hiura (1980) on the basis of a comparative study of wing pattern. A close association or a sistergroup relationship between the genera *Hypermnestra* and *Parnassius* as advocated by several authors (Bryk, 1935 ; Munroe, 1961 ; Ackery, 1975 ; Hancock, 1983), can be supported only by characters which either are evidently plesiomorphic or show a high degree of convergence or homoplasy, such as scaled antennae, the presence of only four radial veins in the fore wing, or the absence of tails on the hindwings.

Secondly, all presumably apomorphic characters that are found in the remaining seven genera of the Parnassiinae are also present in some other taxa of the subfamily Papilioninae, usually in the tribe Troidini. Such characters include the asymmetrical pretarsal claws, which occur as a sexually dimorphic trait most prominent in males of most Parnassiinae (Bischoff, 1932 ; Ackery, 1975). Although all other Papilioninae possess symmetrical pretarsal claws in both sexes, asymmetrical claws have also been found in the Neotropical genus *Parides* of the Troidini (DeVries, 1987 : 64).

In most Parnassiinae, the female abdominal segment VIII has no membranous pleural region, but is more or less completely sclerotized including the gonopore (Miller, 1987b ; Orr, 1988). This condition appears to be correlated with a characteristic mating system. In those genera with a completely sclerotized segment VIII, the females are mated only once and their copulatory opening is permanently sealed after copulation with hardening male secretions, which in some taxa form an externally visible, species-specific structure, a so-called 'sphragis' (Bryk, 1918 ; Orr, 1988).

In the Parnassiinae, an elaborate sphragis occurs only in the genera *Parnassius*, *Bhutanitis* and *Luehdorfia* (Saigusa & Lee, 1982 ; Matsumoto, 1987 ; Miller, 1987b : 380 ; Orr, 1988). However, the female abdominal segment VIII and particularly the region around the gonopore is also entirely sclerotized in *Zerynthia*, *Archon*, *Sericinus*

and *Allancastris*, and there is further evidence for a female monogamous mating system in those taxa including the formation of small mating plugs (Bryk, 1935 ; Orr, 1988 ; Häuser, 1990b). Contrary to statements by Bryk (1931, 1935 : 7), a durable sphragis is not to be found in *Hypermnestra* in which only inconspicuous mating plugs can be observed. A modified segment VIII and sphragis formation also occurs, again, in several groups of the Troidini, most notably in the genera *Cressida* and *Euryades* (Hering, 1932 ; Miller, 1987b ; Orr, 1988 ; Orr & Rutowski, 1991). Furthermore, less conspicuous sphragides are formed in some species of the genera *Atrophaneura* and *Parides*, and in *Trogonoptera* (Munroe, 1961 ; Miller, 1987b : 420 ; Orr, 1988).

In males of all Parnassiinae except *Hypermnestra*, the aedeagus is rather long, thin, distally pointed and heavily sclerotized, which presumably is also in correlation with the mating system. This trait has been interpreted as an autapomorphy of the Parnassiinae by Miller (1987b : 379). The same condition, however, is again observed in certain genera of the Troidini, e.g., *Cressida*, *Euryades*, *Pachliopta*, and to a lesser degree also in the genus *Graphium* (Miller, 1987b ; Orr, 1988).

Another well known character common to both the Parnassiinae and Troidini is the restriction to larval hostplants in the family Aristolochiaceae (Ford, 1944 ; Ehrlich & Raven, 1964 ; Miller, 1987a). These plants contain among other secondary compounds so-called 'aristolochic acids', which are toxic to most other potential herbivores including vertebrates (Hegnauer, 1964 ; Miller & Feeny, 1989). Except for the genera *Parnassius* and *Hypermnestra*, all Parnassiinae have hostplants in the Aristolochiaceae (Bryk, 1935 ; Ackery, 1975), and also all Troidini depend on hostplants in this family (Munroe, 1961 ; Igarashi, 1984 ; Miller, 1987a), whereas no further species of the Papilionidae or other butterflies are known to feed on these plants. Members of both the Parnassiinae and Troidini have been shown to take up and store aristolochic acids, and to be avoided by potential predators (Mell, 1938 ; van Euw *et al.*, 1968 ; Rothschild *et al.*, 1972). The adaptation to hostplants in the Aristolochiaceae coincides in both groups with a peculiar shape of the larvae, which exhibit a characteristic segmental array of fleshy tubercles. This tuberculate larva is restricted to the Parnassiinae and Troidini, whereas most other papilionid larvae are smooth and without tubercles (see Igarashi, 1979). In the Parnassiinae, however, the larvae of the genera *Archon* and *Luehdorfia*, which also live on Aristolochiaceae as hosts, have no tubercles (Le Cerf, 1913 ; Igarashi, 1979).

According to the current view of the phylogeny of the Papilionidae (see Fig. 1), the adaptation to Aristolochiaceae as hostplants, as well as the tuberculate larva, should have arisen twice independently within the same family (Hancock, 1983 ; Miller, 1987a) even though this should seem somewhat unlikely. The alternative interpretation, that this type of larva and hostplant relationship is plesiomorphic for the entire family or, at least, for the Parnassiinae and Papilioninae, has been also put forward by some authors (Ford, 1944 ; Munroe & Ehrlich, 1960 ; Ehrlich & Raven, 1964 ; Scott, 1985), but in this case those characters cannot be simultaneously used to define the Parnassiinae as a monophyletic group. First, other autapomorphous characters would be needed to demonstrate the monophyly of the Parnassiinae, which at present appear not available (Häuser, in prep.). Additional, presumably autapomorphous characters of the Parnassiinae such as elongated labial palpi, and an incurved forewing discocellular vein (Miller, 1987b : 380) are again present in certain Graphiini (Hancock, 1983 ; Miller, 1987b).

The monophyly of the Papilioninae

If the Parnassiinae do not represent a monophylum, the universally accepted monophyly of the Papilioninae must also be called in question. In contrast to the case of the Parnassiinae, a fair number of autapomorphous characters have been cited, which support the monophyly of the Papilioninae (see Munroe, 1961 ; Hancock, 1983 ; Scott, 1985 ; Miller, 1987b). Among the many characters listed, the presence of a meral suture in the metathorax and the occurrence of bristle-like scent scales on the ventral surface of the male hindwing anal region appear most reliable. Miller (1987 : 381) found bristle-like scales at the anal region of the hindwing in several species of *Papilio*, *Meandrusa* and *Teinopalpus* apparently homologous with the well known androconial 'anal brushes' of the Troidini and Graphiini.

Two prominent characters which often are also regarded as true autapomorphies of the Papilioninae, however, show incongruent occurrences. In the male genitalia, a characteristic swallowtail feature is the so-called 'superuncus' or 'pseudouncus' (Ogata *et al.*, 1957), which is a posterior elongation of the male abdominal tergite VIII that covers the uncus dorsally and sometimes even replaces it. Within the Papilionidae, a superuncus is restricted to the Papilioninae (see Miller, 1987b) ; however, it is not a universal character in this subfamily. In most Papilionini and some Troidini the tegumen and the superuncus, i.e., the abdominal tergite VIII, are completely fused into a single hook-

like structure, and the uncus proper appears more or less reduced. Considerable differences exist in the degree of fusion within the two tribes, and in some Papilionini the entire structure is even bi- or trilobed. In most Graphiini, a superuncus is absent and the tegumen and the abdominal tergite VIII are not fused (Munroe, 1961 ; Niculescu, 1978 ; Hancock, 1983 ; Niculescu, 1986 ; Miller, 1987b). This structural diversity has already in the past led to confusing terminology (see Dia-konoff, 1954 ; Ogata *et al.*, 1957 ; Niculescu, 1986), and the homology between different sclerites involved in the formation of the superuncus even within the Papilioninae is still not clearly resolved.

In the venation of the fore wing, the so-called 'basal spur' or cubital cross-vein (cu-v) is generally held to occur among butterflies only in members of the Papilioninae (Munroe & Ehrlich, 1960 : 172 ; Scott, 1985 : 259 ; Miller, 1987b : 381). However, as already noted by Ford (1944 : 218), a clear trace of a basal spur is also present in the genera *Sericinus* and *Bhutanitis* of the Parnassiinae (Munroe, 1961 : 12). Therefore, this character cannot be used as an autapomorphy of the Papilioninae as currently defined, but might rather represent an autapomorphic trait at the family level or, at least, for the Parnassiinae and Papilioninae (Hancock, 1983). Additional characters which have been listed in the literature as possible synapomorphies of the Papi-lioninae, e.g., elongated antennae (Hancock, 1983) or the number of SD setae on the meso- and metathorax in first instar larvae (Scott, 1985), require further comparative studies before reliable phylogenetic inferences can be made.

Conclusions

In summary, the currently accepted hypothesis of the phylogenetic relationships within the family Papilionidae will probably require to be changed. The Parnassiinae as presently defined cannot be recognized as a monophyletic group, and even the removal of the genus *Hyper-mnestra* leaves an apparently non-monophyletic taxon (Häuser, in prep.). The monophyly of the Papilioninae still seems comparatively well established, but some of the characters regarded as autapomorphies for this subfamily cannot be accepted as such. However, there is also no unequivocal evidence available yet for a clearly paraphyletic nature of the Papilioninae nor is it possible to present an alternative, better supported cladogram of the phylogenetic relationships within the Papilionidae solely on the basis of the available information. Clearly, more of the characters employed in previous analyses need to be studied in greater detail to render the polarization of individual character states more reliable.

As a general conclusion, it should be pointed out that foremost the lack of careful examination of individual characters has allowed to criticize the currently accepted view of the phylogeny of the Papilionidae. Although the study of qualitatively different characters such as nucleotide sequences or allozymes should yield additional information, broader comparative morphological studies might not only consume fewer resources than molecular techniques but are still much needed, and will be useful for a better understanding of phylogenetic relationships, probably not only in case of the comparatively well known Papilionidae.

References

- ACKERY, P. R., 1975. A guide to the genera and species of Parnassiinae (Lepidoptera : Papilionidae). *Bull. Br. Mus. nat. Hist., Ent.* 31 (4) : 71-105.
- BISCHOFF, H., 1932. Über einen bisher unbeachteten Sexualcharakter der Parnassier. *Parnassiana* 2 (2) : 16-19.
- BRYK, F., 1918. Grundzüge der Sphragidologie. *Arkiv för Zoologi* 11 (18) : 1-38.
- BRYK, F., 1931. Sphragidologisches. *Parnassiana* 1 (6) : 8.
- BRYK, F., 1934. Baroniidae, Teinopalpidae, Parnassiidae pars I. In : Schulze, F. E., *et al.* (Eds) : Das Tierreich. 64. W. de Gruyter & Co, Berlin, xxiii + 131 pp.
- BRYK, F., 1935. Parnassiidae pars II (Subfam. Parnassiinae). In : Schulze, F. E., *et al.* (Eds) : Das Tierreich. 65. W. de Gruyter & Co, Berlin, li + 790 pp.
- COLLINS, N. M. & MORRIS, M. G., 1985. Threatened Swallowtail Butterflies of the World — The IUCN Red Data Book. IUCN, Gland, vii + 401 pp., pls. 1-8.
- DEVRIES, P., 1987. The Butterflies of Costa Rica and their natural history — Papilionidae, Pieridae, Nymphalidae. Princeton University Press, Princeton, New Jersey, xxii + 327 pp., pls. 1-50.
- DIKONOFF, A., 1954. Considerations on the terminology of the genitalia in Lepidoptera. *Lep. News* 8 : 67-74.
- EHRlich, P. R. & RAVEN, P. H., 1964. Butterflies and plants : a study in coevolution. *Evolution* 18 : 586-608.
- EUW, J. VAN, REICHSTEIN, T. & ROTHSCHILD, M., 1968. Aristolochic acid-I in the swallowtail butterfly *Pachlioptera aristolochiae* (Fabr.) (Papilionidae). *Israel J. Chem.* 6 : 659-670.
- FORD, E. B., 1944. Studies on the chemistry of pigments in the Lepidoptera, with reference to their bearing on systematics. 4. The classification of the Papilionidae. *Trans. R. ent. Soc. Lond.* 94 : 201-223.

- GOYLE, S., 1990. Anatomy of the Common Lemon Butterfly *Papilio demoleus demoleus* (L.). Today & Tomorrow's Printers and Publishers, New Delhi, xii + 151 pp.
- HÄUSER, C. L., 1990a. Probleme der phylogenetischen Systematik am Beispiel der Parnassiinae (Lepidoptera, Papilionidae). *Verh. Deut. Zool. Ges.* 83 : 506.
- HÄUSER, C. L., 1990b. Vergleichende Untersuchungen zur Morphologie, systematischen Bedeutung und Phylogenese der weiblichen Genitalorgane der Lepidoptera (Insecta). Unveröffentlichte Dissertation, Universität Freiburg, 229 pp., figs. 1-110.
- HÄUSER, C. L., in prep. A re-evaluation of the phylogenetic relationships of the genera of the Parnassiinae (Lepidoptera : Papilionidae).
- HANCOCK, D. L., 1983. Classification of the Papilionidae (Lepidoptera) : a phylogenetic approach. *Smithersia* 2 : 1-48.
- HEGNAUER, R., 1964. Chemotaxonomie der Pflanzen. Band 3. Birkhäuser Verlag, Basel, 743 pp.
- HIURA, I., 1980. A phylogeny of the genera of Parnassiinae based on analysis of wing pattern, with description of a new genus (Lepidoptera : Papilionidae). *Bull. Osaka Mus. Nat. Hist.* 33 : 71-95.
- IGARASHI, S., 1979. Papilionidae and their early stages [in Japanese]. 2 vols. Tokyo.
- IGARASHI, S., 1984. The Classification of the Papilionidae mainly based on the Morphology of their Immature Stages. *Tyô to Ga* 34 (2) : 41-96.
- LE CERF, F., 1913. Contribution à la faune lépidoptérologique de la Perse (Catalogue des Rhopalocères). *Annales d'Histoire Naturelle*, 2 (Entomologie), 2 : xii+88 pp., pls. 1-2.
- MATSUMOTO, K., 1987. Mating patterns of a sphragis-bearing butterfly, *Luehdorfia japonica* Leech (Lepidoptera : Papilionidae), with descriptions of mating behaviour. *Res. Popul. Ecol.* 29 : 97-110.
- MELL, R., 1938. Beiträge zur Fauna sinica. XVII. Inventur und ökologisches Material zu einer Biologie der südchinesischen Lepidopteren. *Deutsche Entomologische Zeitschrift* 1938 (2) : 197-345.
- MILLER, J. S., 1987a. Host-plant relationships in the Papilionidae (Lepidoptera) : Parallel cladogenesis or colonization? *Cladistics* 3 (2) : 105-120.
- MILLER, J. S., 1987b. Phylogenetic studies in the Papilioninae (Lepidoptera : Papilionidae). *Bull. Amer. Mus. Nat. Hist.* 186 : 365-512.
- MILLER, J. S. & FEENY, P. P., 1989. Interspecific differences among swallowtail larvae (Lepidoptera : Papilionidae) in susceptibility to aristolochic acids and berberine. *Ecol. Entomol.* 14 : 287-296.
- MUNROE, E., 1961. The Classification of the Papilionidae (Lepidoptera). *Can. Ent.*, Suppl. 17 : 1-51.
- MUNROE, E. & EHRLICH, P. R., 1960. Harmonization of concepts of higher classification of the Papilionidae. *J. Lepid. Soc.* 14 : 169-175.

- NICULESCU, E. V., 1978. Recherches morphologiques et systématiques sur les Papilioninae (Lepidoptera-Papilionidae) (II). *SHILAP Revia lepid.* 6 (23) : 179-193.
- NICULESCU, E. V., 1986. L'armature génitale mâle des Papilionidae (Lepidoptera - Aparasternia). *Bull. Cerc. Lépidopt. Belg.* 15 (4) : 46-59.
- OGATA, M., OKADA, Y., OKAGAKI, H. & SIBATANI, A., 1957. Male Genitalia of Lepidoptera : Morphology and Nomenclature III. Appendages Pertaining to the Tenth Somite. *Ann. Ent. Soc. America* 50 : 237-244.
- ORR, A. G., 1988. Mate conflict and the evolution of the sphragis in butterflies. Unpublished Ph.D. thesis, Griffith University, Nathan, Queensland, xvi + 348 pp.
- ORR, A. G. & RUTOWSKI, R. L., 1991. The function of the sphragis in *Cressida cressida* (Fab.) (Lepidoptera, Papilionidae) : a visual deterrent to copulation attempts. *J. Nat. Hist.* 25 : 703-710.
- ROTHSCHILD, M., EUW, J. VAN & REICHSTEIN, T., 1972. Aristolochic acids stored by *Zerynthia polyxena* (Lepidoptera). *Insect Biochem.* 2 : 334-343.
- SAIGUSA, T. & LEE, C., 1982. A rare papilionid butterfly *Bhutanitis mansfieldi* (Riley), its rediscovery, new subspecies and phylogenetic position. *Tyô to Ga* 33 : 24.
- SCOTT, J. A., 1985. The Phylogeny of Butterflies (Papilionoidea and Hesperioidea). *J. Res. Lepid.* 23(4) : 241-281.